

Shell Repair Frequencies of Two Intertidal Gastropods from Northern California: Microhabitat Differences

by

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Abstract. *Tegula funebris* (A. Adams, 1854) and *Nucella emarginata* (Deshayes, 1839) from distinct microhabitats (surge channels, tidepool, and mussel bed) at Bodega Bay, California, were examined, and shell repairs enumerated. Frequencies of repair in samples of *Tegula* from each microhabitat were significantly different from each other. All samples of *Nucella* differed from each other except those from Surge Channel 2 and the mussel bed site. The significance of these results for interspecific comparisons of shell-repair frequencies is discussed.

INTRODUCTION

THE FREQUENCY OF shell repair in populations of intertidal gastropods has been used recently as an indicator of intensity of selection for antipredator traits (VERMEIJ, 1978, 1981, 1982a). Briefly, repairs are records of sublethal attacks by predators (or other shell-breaking agents), and snails that survive such attacks will contribute more progeny to subsequent generations than those which succumb (VERMEIJ, 1982b). Hence, where shell-repair frequencies are high, it is inferred that selection for antipredator traits is high. Shell breakage from agents other than predation should, by the same reasoning, select for some of the same shell characters. However, many morphological features are identified as defense primarily against predation, and scars left by predators are often distinguishable from other markings (VERMEIJ, 1978). Analysis of shell repair in various gastropods (VERMEIJ, 1978) and, in more detail, of terebrid snails (VERMEIJ *et al.*, 1980) reveal that repair frequencies are highest at low latitudes and, between oceans, in the Indo-West Pacific. These findings support other evidence that predation is a greater hazard to snails in the tropics than to those of temperate shores (VERMEIJ, 1978; ZIPSER & VERMEIJ, 1978; BERTNESS *et al.*, 1981; MENGE & LUBCHENCO, 1981). There are, however, possible problems with the use of shell-repair frequencies as an indicator of predation intensity, including small sample sizes, frequent reliance on museum collections, and microhabitat-related intraspecific variation in repair frequency. The purpose of this note is

to present data on intraspecific variation in shell-repair frequency.

MATERIALS AND METHODS

Tegula funebris (A. Adams, 1854) and *Nucella emarginata* (Deshayes, 1839) were collected in the intertidal zone adjacent to the Bodega Marine Laboratory (BML) near Bodega Bay on the northern California coast. The intertidal zone at BML consists of highly jointed granitic benches. Live snails were collected at four distinct microhabitats. Specimens of *Tegula* were collected at two surge channels and in a bed of the mussel *Mytilus californianus* Conrad, 1837. Specimens of *Nucella* were collected at the two surge channels, in the mussel bed, and also on a vertical rock surface near a mid-intertidal tidepool. Each snail was examined with a low-power binocular dissecting microscope. Shell repairs were identified as jagged relief on the surface of the body whorl. The extreme unevenness of scars distinguish them from growth lines, which may be prominent on these shells. Further, many scars are of a characteristic shape produced by the peeling action of the crabs (see VERMEIJ, 1978). Where ambiguity existed as to the origin of a marking, that shell was scored as not-scarred. Voucher specimens from each sample were retained.

RESULTS

Frequencies of shell repairs for *Tegula* were dramatically higher in the samples from the surge channels than in the

Table 1

Percentages of *Tegula* and *Nucella* shells with shell repairs, with sample size in parentheses. Code for microhabitats: surge channel 1 = SC1, surge channel 2 = SC2, mussel bed = MB, tidepool = TP.

	SC1	SC2	MB	TP
<i>Tegula</i>	49.6 (250)	28.5 (200)	3.8 (177)	—
<i>Nucella</i>	19.6 (234)	10.0 (200)	9.3 (236)	5.5 (200)

samples from the mussel bed: 123 of 250 and 57 of 200 shells from the surge channels had scars compared to 7 of 177 from the mussel bed (Table 1). Chi-square analysis shows that each sample differs significantly from the other two (Table 2). For *Nucella*, like *Tegula*, the samples from the surge channels had the highest repair frequencies, with the mussel-bed and tidepool samples next in descending order. However, only Surge Channel 1 was significantly different than the others (Table 2).

Interspecific comparison shows that *Tegula* is significantly more scarred in the surge channel microhabitats, whereas *Nucella* is more scarred in the mussel bed (Table 2).

DISCUSSION

These results show shell-repair frequencies can vary between microhabitats. To interpret interspecific differences in shell-repair frequencies meaningfully, a range of microhabitats should be sampled. For example, a possible misinterpretation based on mussel-bed samples would be that *Nucella* is more scarred than *Tegula*; whereas data pooled from several microhabitats show that *Tegula* is significantly more scarred ($\chi^2 = 79.2$, $P < 0.001$). Hence, discussion of the significance of differences in shell-repair frequencies should treat *Tegula* as the more scarred species. Although this study is not intended as a test of hypotheses of gastropod shell evolution, it is clear from the arguments outlined in the Introduction that one would expect selection for antipredatory traits to be higher for *Tegula*. However, *Tegula*, a typical trochid, possess few structural features identifiable as antipredatory. In contrast, *Nucella* has a narrow aperture and a short spire, both identified as defensive (VERMEIJ, 1978). This apparent discrepancy may be a result of an invalid comparison of phylogenetically distant species; morphological constraints and potential evolutionary responses may not be similar for both species.

At present I can only speculate on the source of variation in scar frequency reported here. The surge channel microhabitats might be more accessible to mobile predators (e.g., crabs and fishes) compared to mussel beds due

Table 2

Chi-square test with continuity correction of differences in shell-repair frequencies between each sample. Code for microhabitats as in Table 1, except prefaced by *T* (= *Tegula*) or *N* (= *Nucella*). All values are significant at $P < 0.05$ except where marked ns ($P > 0.05$).

	TSC1	TSC2	TMB	NSC1	NSC2	NMB	NTP
TSC1	—	19.7	103.3	46.2	78.3	91.8	100.8
TSC2	—	—	40.3	4.2	20.8	25.6	35.9
TMB	—	—	—	22.0	4.7	4.1	0.3 ns
NSC1	—	—	—	—	7.1	9.3	17.7
NSC2	—	—	—	—	—	0.006 ns	2.2 ns
NMB	—	—	—	—	—	—	1.74 ns

to unbroken connection with lower-intertidal and subtidal levels, and perhaps due to its horizontal aspect facilitating predator movement. For example, while diving in other nearby surge channels, I have observed the large rock crab *Cancer antennarius* Stimpson, 1856, to be abundant. Similar densities are expected in the surge channels reported on here. Further, wave action may at times be intense, resulting in nonpredator-induced shell breakage. Lower frequencies of shell repair in the mussel bed for *Tegula* and tidepool for *Nucella* may be due to refuge from predators and wave shock afforded by these microhabitats. The reversed trend of shell breakage frequency in the mussel bed remains an interesting problem. Probable durophagous predators in the mussel bed are the black oystercatcher, *Haematopus bachmani* Audubon, and the lined shore crab, *Pachygrapsus crassipes* Randall, 1839; however, no data are available on preferences of these predators for *Tegula* or *Nucella*.

Finally, some repair frequencies reported here are high compared with those reported for temperate and even some tropical snails. For instance, VERMEIJ *et al.* (1980) report average frequencies of 0.25–0.96 (where multiple scars on a shell are counted) for tropical terebrids, and 0.28 for temperate species. Frequencies reported for other temperate species are lower (VERMEIJ, 1978). The data presented here and elsewhere (REIMCHEN, 1982; VERMEIJ, 1982a) do not contradict conclusions about latitudinal predation patterns, but they do show that shell breaking agents can be locally intense in temperate as well as tropical gastropod assemblages.

ACKNOWLEDGMENTS

I thank Director Cadet Hand and the staff at the Bodega Marine Laboratory for providing space and use of the fine facilities there. I also thank D. C. Edwards for a critical and helpful review of the manuscript. This is a contribution of the Center for Ecological Education and Research.

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